JOURNAL OF THE ARNOLD ARBORETUM VOL. 47

THE CORNACEAE IN THE SOUTHEASTERN UNITED STATES¹

106

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CORNACEAE Dumortier, Anal. Fam. Pl. 33, 34. 1829, "Corneae," nom. cons. (DOGWOOD FAMILY)

Trees or shrubs [rarely perennial herbs]. Flowers small, bisexual [unisexual in dioecious species], regular. Floral tube adnate to the ovary; calyx lobes small to obsolete. Petals 4 [5], [rarely absent], inserted on an epigynous disc. Stamens equal in number to the petals and alternate with them. Ovary inferior, 1-4-locular, with a single pendulous, anatropous ovule in each locule. Fruit a drupe [rarely a berry]. Embryo straight; endosperm copious. (Excluding Alangiaceae DC., Garryaceae Lindl., and Nyssaceae Dumort.) TYPE GENUS: Cornus L.

A rather heterogeneous family of seven to sixteen genera, depending upon the generic and familial concepts adopted, with about 100 species, mainly in north-temperate regions, a few in the Tropics, in Africa, Madagascar, South America, and also in New Zealand; only Cornus occurs in eastern North America.

The family has been placed in the Umbellales on the basis of its fewcarpellate inferior ovary, reduced calyx, and tendency toward a manyflowered umbellate inflorescence. The anatomy of Cornaceae differs in many respects from that of the Umbelliferae and Araliaceae, but the secretory ducts and extrorse micropyle of Mastixia Blume are thought by some authors to link Cornaceae with Araliaceae. Biochemical studies have shown aucubin to be present in Cornaceae but absent from Umbelliferae and Araliaceae. Garryaceae, Alangiaceae, and Nyssaceae are very closely re-

¹ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. The treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References marked with an asterisk have not been seen by the author.

I am grateful to Dr. Wood for his generous suggestions and valuable criticisms and to Dr. George K. Brizicky for his patient guidance and discussion. I am also grateful to Dr. R. H. Eyde for his comments on the manuscript. The typescript was prepared by Mrs. Gordon W. Dillon, and the plate is the work of Arnold D. Clapman.

1966] FERGUSON, CORNACEAE 107

lated families more or less recently segregated from the Cornaceae. Although studies by Moseley and Beeks and by Eyde (1964) confirm the affinity of Garryaceae with Cornaceae, the highly specialized amentiferous structure of its inflorescence appears to justify treating the group as a separate family. Nyssaceae and Cornaceae have been grouped together as the Cornales, but on the basis of their valvate petals Hutchinson places Cornaceae and Araliaceae (one tribe of which has imbricate petals) in an order Araliales next to the Cunoniales and distinct from the Umbelliferae, which have imbricate petals. Serological studies on Nyssa L., Davidia Baill., and Cornus may be interpreted to support the separation of Nyssaceae from Cornaceae. In anatomy and morphology the Cornaceae resemble the Caprifoliaceae in many ways, and the pollen, in particular, is similar to that of Viburnum and Sambucus. Metcalfe and Chalk draw attention to a similarity between Cornaceae and Hydrangeaceae in wood anatomy. Within the family, Harms separated the subfamilies Curtisioideae and Mastizioideae, both with seeds with an adaxial (ventral) raphe, from the Cornoideae, which have seeds with an abaxial (dorsal) raphe. Wangerin divided the Cornoideae into four tribes: Toricellieae, Helwingieae, Corneae, and Griselineae. The Toricellieae and Helwingieae are considered distinct families by some workers, and studies of pollen morphology (Chao) and wood anatomy (Li & Chao) support this treatment. On the basis of wood anatomy, Adams has proposed the removal of Aucuba Thunb. and Kaliphora Hook. f. to separate tribes. The position of Corokia A. Cunningh, is doubtful (cf. Eyde). Engler places it near Argophyllum J. R. & G. Forst. in the Saxifragaceae subfam. Escallonioideae. Eyde, on the basis of floral anatomy, rejects the assignment of Corokia to Cornaceae, but questions certain points in Engler's alternative taxonomic treatment. Pollination is probably by insects; Griselinia Gmel. is believed to be wind pollinated, but at least one species produces nectar (Percival, New Phytol. 60: 235. 1961). Some species of Helwingia Willd., Corokia, Griselinia, Aucuba, and many species of Cornus are cultivated for their ornamental value; and some also possess medicinal properties. Curtisia dentata (Burm. f.) C. A. Sm. (C. jaginea Ait.) is a useful African hardwood tree.

Chromosome numbers of 2n = 16, 18, 20, 22, 27, 32, 36, 44, ca. 72, 120, and 144 have been reported.

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108

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1966] FERGUSON, CORNACEAE 109

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1. Cornus Linnaeus, Sp. Pl. 1: 117. 1753; Gen. Pl. ed. 5. 54. 1754.

Deciduous trees or shrubs [rarely perennial herbs]. Leaves opposite, rarely alternate, simple, usually petiolate, exstipulate; blade entire, or obscurely serrate, pinnately veined, often pubescent, the lower surface occasionally covered with a fine network of short hairs or papillae and sometimes with appressed, erect, or curling, simple or characteristic bifid hairs. Inflorescences terminal or axillary, dichotomously branched, ebracteate cymes or panicles, [or bracteate umbelliform cymes,] or heads (reduced cymes) surrounded by petal-like involucral bracts and an inner ring of small, obtuse, membranaceous bracteoles. Flowers bisexual [unisexual in dioecious species], epigynous, sessile or short pedicellate. Floral tube turbinate, urceolate or campanulate, adnate to the ovary; calyx lobes 4, distinct or obsolete. Petals 4, valvate in bud, inserted on the margin of a fleshy nectariferous disc, oblong or ovate, white, purple, or yellow.

110 JOURNAL OF THE ARNOLD ARBORETUM [vol. 47

Stamens 4, exserted; filaments filiform or subulate; anthers oblong, 2locular, dorsifixed, versatile, introrse, longitudinally dehiscent; pollen small or medium, prolate, tricolporate, reticulate or granular [occasionally united in tetrads]. Gynoecium (1)2(3)-carpellate, syncarpous; style single, filiform or columnar, sometimes dilated below the stigma; stigma capitate or truncate; ovary inferior, adnate to the floral tube and to the disc, (1)2(3)-locular, 1 locule sometimes aborting; ovules solitary in each locule, pendulous, anatropous, with abaxial raphe, micropyle superior. Fruit a globose, ellipsoid, or ovoid drupe; stone 2(rarely 1)-seeded, furrowed, rarely with a distinct pit at the apex. Seeds oblong, compressed; endosperm copious; embryo as long as the endosperm, straight, the cotyledons foliaceous, radicle terete and near the micropyle. Embryo sac development of the Fritillaria type in some species, reported to be of the normal (Polygonum) type in others. (Including Afrocrania (Harms) Hutchins., Benthamidia Spach, Bothrocaryum (Koehne) Pojark., Chamaepericlymenum Hill, Dendrobenthamia Hutchins., Swida Opiz.²) LECTO-TYPE SPECIES: C. mas L.; see B. C. Dumortier, Florula Belgica 83. 1827, and P. A. Rydberg, Bull. Torrey Bot. Club 33: 147. 1906.³ (Name from Latin, cornu, a horn, presumably because of the hardness of the wood.) -DOGWOOD.

A genus of about 60 species, mainly of temperate regions of the Northern Hemisphere, but extending to Central and South America, with one species in Africa; some 17 species in North America and about six in our area. The treatment of the genus has varied widely, some authors recognizing a number of segregate genera, others treating these divisions as either subgenera or sections. Eight subgenera compose the genus as delimited here (cf. Ferguson, Jour. Arnold Arb. 47: 100–105. 1966); four are represented in the United States, and three in our area. Only the correct sectional or generic names are given here as synonyms of the subgenera. All but two of the species in the southeastern United States are members of subg. KRANIOPSIS Raf. (sect. *Thelycrania* Dumort.; *Swida* Opiz), characterized by ebracteate cymose or paniculate inflorescences appearing

² Although usually given as Svida and originally published as Swida, the orthography used here seems to be most in accord with the International Code (Art. 73, Note 6), which prescribes the change from "j" to "i," thus making the name pronounceable. ³ Hutchinson (Ann. Bot. II. 6: 83-93. 1942) proposed Cornus sanguinea L. as lectotype species because it is a more typical representative of the genus and because C. mas L. was removed to the genus Macrocarpium Nakai (Bot. Mag. Tokyo 23: 38. 1909). He incorrectly cited Britton and Brown (Illus. Fl. No. U. S. 2: 660. 1913) as the earliest authors to select C. mas as lectotype species. Rehder (Bibliogr. Cult. Trees Shrubs 496. 1949) also adopted C. sanguinea as lectotype. However, Cornus was effectively typified by Dumortier (Florula Belgica 83. 1827) when he established the section Cornotypus which included only C. mas. Rydberg selected C. mas as lectotype species in 1906, and, in 1908, Britton (N. Am. Trees 741), a year earlier than Nakai proposed his genus Macrocarpium, also selected the same species. Furthermore, C. sanguinea is a component of both Swida Opiz (Berchtold & Opiz, Oekon.-tech. Fl. Böhmens 2: 174. 1838) and Thelycrania (Dumort.) Fourreau (Ann. Soc. Linn. Lyon II. 16: 394. 1868).

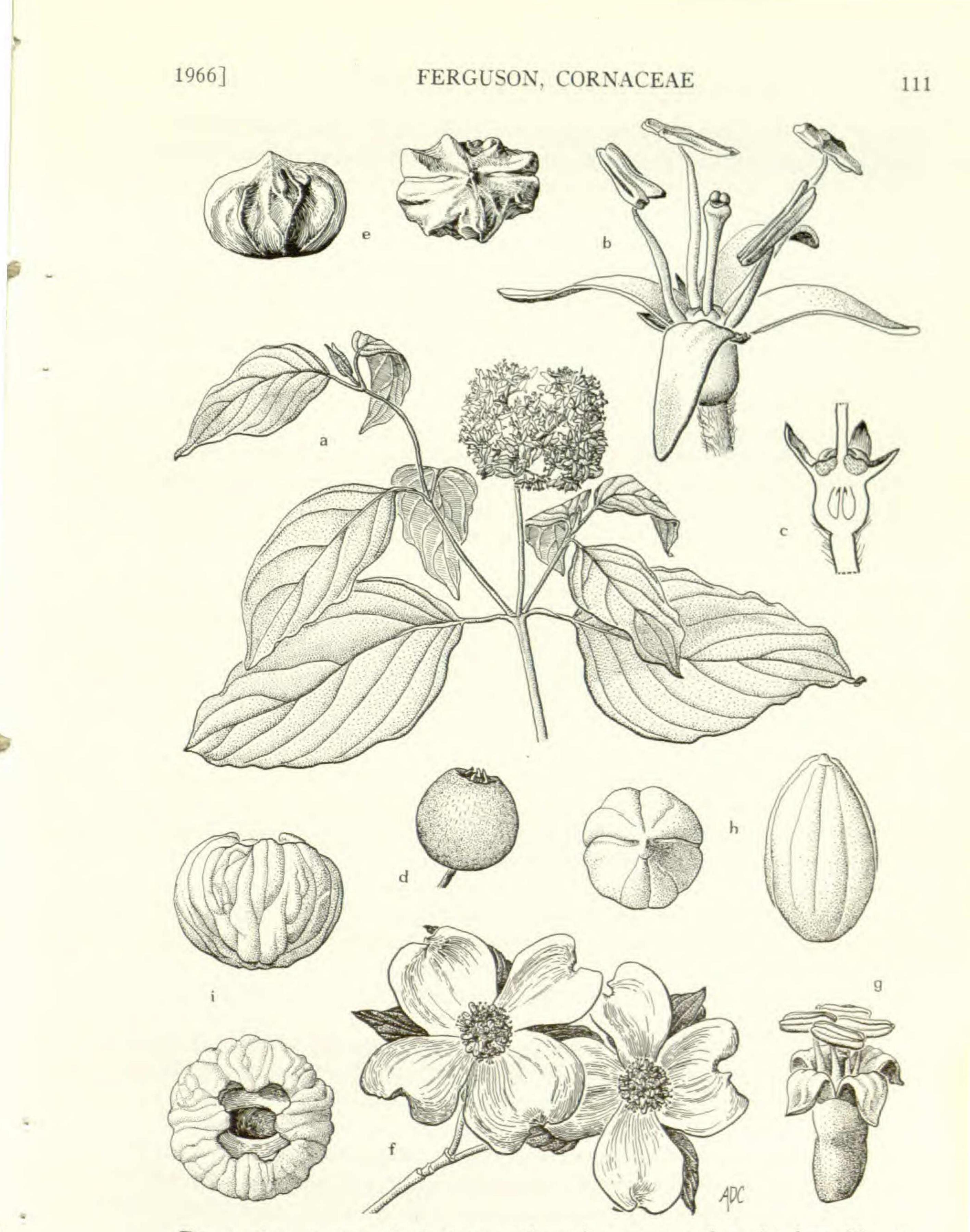


FIG. 1. Cornus. a-e, C. Amomum subsp. Amomum: a, flowering branchlet, \times 1/2; b, flower, \times 6; c, flower (with petals and stamens removed) in semidiagrammatic vertical section to show nectariferous disc and two-locular ovary with solitary, pendulous ovules, \times 6; d, mature drupe, \times 2; e, stone in lateral view and from above, \times 4. f-h, C. florida: f, flowering branchlet seen from above, \times 1/2; g, flower, \times 4; h, stone from above and in lateral view, \times 4. i, C. alternifolia: i, stone in lateral view and from above to show apical pit.

112 JOURNAL OF THE ARNOLD ARBORETUM [VOL. 47

with or after the foliage. Cornus Amomum Mill. (Swida Amomum (Mill.) Small), distinguished by its usually blue fruit, smooth leaves, dilated style, brown pith, and long calyx lobes, is represented with us by two subspecies treated as distinct species by some authors. Subspecies Amomum, 2n =22, with leaves rounded at the base and green on the lower surface, extends from southern New England, west to southern Illinois and Kentucky, and south to Tennessee, the Carolinas, Georgia, Alabama, and northern Mississippi; subsp. obliqua (Raf.) J. S. Wilson, 2n = 22, characterized by cuneate leaf bases and white papillae on the lower surfaces of the leaves, occurs from northwestern New England and adjacent Canada, westward to North Dakota, Kansas, and Nebraska, and south to Arkansas and western Tennessee. Cornus asperifolia Michx. and C. Drummondii C. A. Meyer (Swida asperifolia sensu Small, S. Priceae Small) are distinguished from other species in the subgenus by their scabrid upper leaf surfaces. These two species are closely related, although Wilson has treated the former as a subspecies (microcarpa (Nash) J. S. Wilson) of C. foemina. Cornus microcarpa Nash (Swida microcarpa (Nash) Small) appears to be only a variant of C. asperifolia. Cornus Drummondii, occurring from Alabama and western Tennessee to Texas, Arkansas, Nebraska, and Ontario, is separated by its white drupes and white papillose indumentum on the lower surface of the leaves from C. asperifolia, a species of the southeastern Coastal Plain from Florida to Georgia, South Carolina, and Alabama with blue drupes and nonpapillose leaves.

The complex Cornus foemina Mill. is distinctive in its smooth twigs and the smooth upper surface of the leaves. Subspecies foemina (Swida stricta (Lam.) Small), characterized by blue fruits, usually flat-topped inflorescences, and red young branches, occurs throughout the southeastern United States and extends to Delaware, Indiana, and Texas. Some workers regard the closely allied *C. racemosa* Lam. (white fruit, usually convex inflorescences, and brown young branches) as occurring in the southeastern United States, but the treatment followed here is that of Wilson, who regards this taxon as *C. foemina* subsp. racemosa (Lam.) J. S. Wilson with a distribution to the north of our area. The frequent hybridization between species of subg. KRANIOPSIS often makes identification difficult. The color of the pith and of the fruit, important taxonomic characters for distinguishing between some of the subspecies, should be recorded by collectors.

The similar subg. MESOMORA Raf. (sect. Bothrocaryum (Koehne) Harms ex Nakai; Bothrocaryum (Koehne) Pojark.) is distinctive in the alternate leaves, stones with a characteristic deep apical pit, and chromosome number. It includes only Cornus controversa Hemsl., 2n = 20, of eastern Asia, and C. alternifolia L. (Swida alternifolia (L.) Small), 2n =20, widespread in the northeastern United States and adjacent Canada and extending southward through eastern Tennessee, the Carolinas, Georgia, and Alabama to northwestern Florida (Gadsden County), and westward to Minnesota and northern Arkansas. 12

1966] FERGUSON, CORNACEAE

Subgenus CYNOXYLON (Raf.) Raf. (sect. Cynoxylon Raf.; Benthamidia Spach; Cynoxylon (Raf.) Small), characterized by woody habit, flowers aggregated into sessile heads surrounded by large, white, petaloid involucral bracts, and free, thin-fleshed drupes, is represented by Cornus florida L. (Cynoxylon floridum (L.) Small), 2n = 22, widespread in our area (but probably absent from southern Florida) and extending north to southern Maine and Ontario, and west to eastern Texas and Kansas, with the disjunct but doubtfully distinct var. Urbiniana (Rose) Wangerin in Mexico (Nuevo Léon and Veracruz). A calciphile, it is one of the most characteristic and conspicuous spring-flowering trees of the eastern United

113

States.

The herbaceous subg. ARCTOCRANIA Endl. ex Reichenb. (sect. Cornion Spach; Chamaepericlymenum Hill) is represented in the eastern United States by Cornus canadensis L., bunchberry, 2n = 44, of transcontinental distribution northward and sporadic occurrence southward to California and New Mexico, in the West, and to Pocahontas County, West Virginia, in the East. Wherry has suggested that the migration of *C. canadensis* southward "is restricted by its inability to establish itself in soils which are heated above 65° [F.] [18° C.] during the summer."

The morphological relationships between the subgenera appear to be reticulate. (See also Rickett, 1950.) A number of interspecific hybrids are known, but only a single hybrid between subgenera, Cornus \times acadiensis Fern. (C. alternifolia \times C. stricta [C. stolonifera]), has been recorded. Basic chromosome numbers of 9, 10, and 11 have been reported: 2n = 18in subg. CORNUS; 20 in MESOMORA; 22 in BENTHAMIA, CYNOXYLON, and KRANIOPSIS; and 22 or 44 in ARCTOCRANIA. (A triploid count of 27 has also been recorded for C. mas, 2n = 18.) Serological studies support the distinctness of subg. ARCTOCRANIA, CYNOXYLON, and KRANIOPSIS but show a close relationship between subg. BENTHAMIA (C. Kousa Buerger ex Miq., 2n = 22) and subg. CYNOXYLON (C. florida and C. Nuttallii Audubon). Flowers are usually homogamous, but may be proterandrous in subg. ARCTOCRANIA (e.g., Cornus suecica L., 2n = 22), with exposed nectar secreted by the epigynous disc surrounding the style. Pollination is probably accomplished by insects, including small creeping Coleoptera and some Diptera and Hymenoptera. Cross-pollination is favored by the differing lengths of style and stamens, but self-pollination may also occur by the spreading of the stamens to touch neighboring flowers.

Fossils of *Cornus* have been reported from late Cretaceous, Tertiary, and Pleistocene strata. The remains include leaf impressions, stones,

wood, and pollen.

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Many species, especially *Cornus florida*, are cultivated as ornamentals. *Cornus florida* contains a bitter principle, cornine, which has been used for its medicinal properties. The wood of some species is valuable for its hard, smooth, fine texture and is used for tool handles, cotton reels, meat skewers, and charcoal.

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1966] FERGUSON, CORNACEAE 115

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116 JOURNAL OF THE ARNOLD ARBORETUM [vol. 47

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